THE EFFECT OF TEMPERATURE ON THE ACTIVITY OF BLUEFISH, *POMATOMUS SALTATRIX* L.[1]

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Temperature is one of the most important environmental stimuli exerting an influence on the natural habits of marine organisms. An understanding of the precise role played by this ubiquitous stimulus on the activity of a species is of both fundamental and applied importance. Our aim in this work is to examine, quantitatively, under controlled laboratory conditions, the way in which changes in temperature act upon established behavior patterns in a marine pelagic species. Although there is considerable literature on the responses of fish to temperature (for reviews see Fry, 1964, 1967; de Sylva, 1969; for bibliographies see Kennedy and Mihursky, 1967; Raney and Menzel, 1969; Coutant, 1969, 1970b); there appear to be few published accounts on the subtle changes in behavior of marine pelagic species induced by slowly changing temperature.

Using previously established changes in swimming speed and schooling behavior as our criteria for normal activity of a small group of adult bluefish, *Pomatomus saltatrix* (Olla and Studholme, 1972), we measured the effects of a gradual rise and fall in temperature. Our goal was to predict, with some confidence, the effects of particular thermal levels on natural populations.

MATERIALS AND METHODS

The subjects of our studies were six adult bluefish, 55–65 cm, held in a 121 kl aquarium under conditions of controlled light and temperature (Olla, Marchioni and Katz, 1967). A specialized lighting system simulated natural diurnal changes in light intensity and duplicated natural seasonal photoperiod. Salinity ranged from 23.0–24.5‰ and oxygen from 3.5–6.3 ml/l. Several months after the fish were introduced into the tank, they were in a healthy condition, free of any external signs of infection and feeding regularly.

Since our aim was to observe changes in speed and schooling tendency in free-swimming animals, the number of fish used was important. Based on the space limitations of the tank, preliminary observations indicated that 6–8 adult bluefish constituted a group small enough to avoid crowding yet large enough to be reflective of real changes in speed and grouping.

We conducted the following studies to observe the effects of both a gradual increase and decrease of temperature on swimming speed and schooling tendency. Our speed measurements consisted of five stopwatch readings made every hour of the time for the lead fish of the largest group to swim a measured distance (335 cm). We used the median of these readings for subsequent analysis. We mea-

sured the tendency to school by recording, at the same time of the speed readings, the largest number of fish swimming together in the same direction at relatively the same speed within three body lengths. The medians of these counts were used to determine changes in schooling tendency.

We raised and lowered water temperature by controlling room temperature and water inflow, which resulted in a variation of about ±0.2° C throughout the tank.

We fed the fish live mummichogs, *Fundulus heteroclitus,* 50–125 mm, following the procedures outlined in a previous study (Olla, Katz and Studholme, 1970).

Low temperature

In this experiment we observed the effects of a gradual decrease in temperature on the activity of the fish for 29 days under a natural seasonal photoperiod ranging from 11.16–10.30 hr. The rate of decrease ranged from 0.004–0.042°C/hr (mean 0.012° C) with the exception of 2 days when, due to operational problems, the temperature remained at 14.9° C. Holding temperatures for the fish preceding the experiment were as follows: third month, 22.5 ± 0.5° C; second month, 22.0 ± 0.5° C; first month, 21.0 ± 1.0° C. Then for 18 days prior to the temperature decrease, we held the fish at 19.5 ± 0.5° C and at a light regimen corresponding to the natural seasonal photoperiod during which their rhythmic activity, schooling and feeding showed day-to-day stability. We will refer to this temperature (19.5° C) as the acclimation level (Fry, 1967) for this experiment. At the low temperature limit at which signs of stress were evident (as determined by significant changes in swimming speed and schooling tendency) the temperature remained constant for 24 hours and then increased (mean 0.023° C/hr) until the fish no longer showed signs of stress. Then we lowered the temperature (mean 0.024° C/hr) and when stress became apparent, raised it (mean 0.023° C/hr) toward the acclimation level. Following each 4-day set of observations, while the temperature continued to change, the fish were fed to satiation. Measurements on speed and schooling were suspended during feeding and were resumed 56–60 hr later.

High temperature

In this experiment we observed the effects of a gradual increase in temperature over a 32-day period under a natural seasonal photoperiod ranging from 15.75–16.20 hr. The rate of increase ranged from 0.002–0.038° C/hr (mean 0.021° C. Holding temperatures for the fish preceding the experiment were as follows: third month, 20.0 ± 1.0° C; second month, 20.0 ± 0.6° C; first month, 19.9 ± 0.7° C). Then for 21 days prior to the temperature increase, we held the fish at 19.9 ± 0.5° C and at a light regimen corresponding to the natural seasonal photoperiod. We will refer to this temperature (19.9° C) as the acclimation level for this experiment. At the upper temperature limit as determined by the stress responses of the fish, the temperature was held constant for 6 days and then gradually decreased (mean 0.020° C/hr). Following each 4-day set of observations, we held the temperature constant and fed the fish to satiation. Measurements resumed 29–30 hr later.
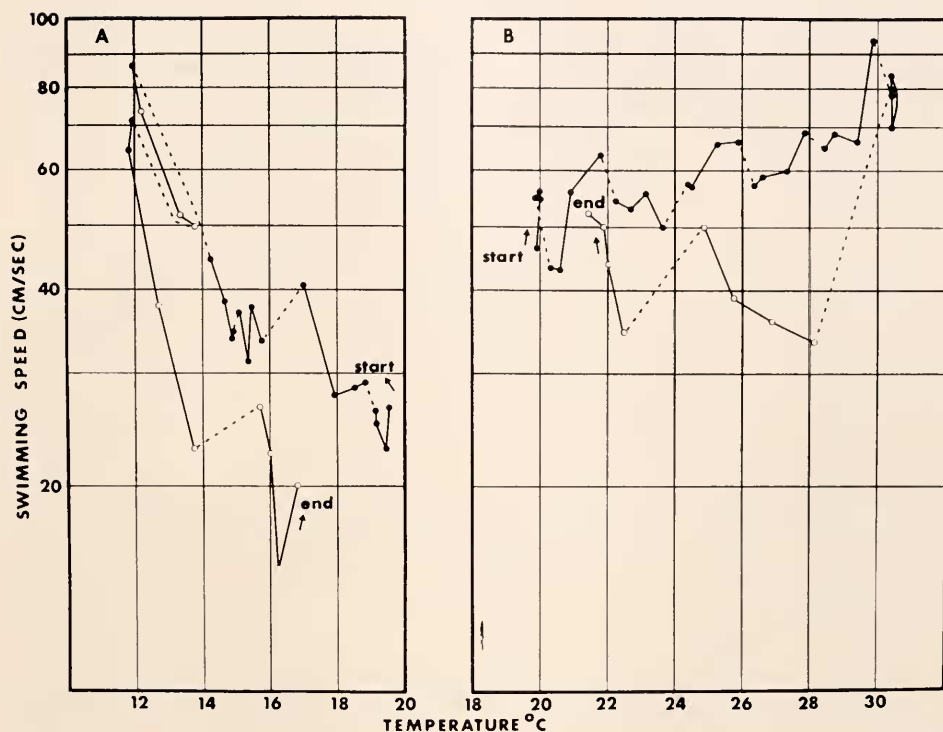
FIGURE 1. (A) Mean daily swimming speeds recorded during low temperature experiment under photoperiods ranging from 11.16–10.30 hr. Black circles represent speeds measured during decreasing temperature; open circles, speeds measured during increasing temperature; dotted lines indicate 72-hr interval. (B) Mean daily swimming speeds recorded during high temperature experiment under photoperiods ranging from 15.75–16.20 hr. Black circles represent speeds measured during increasing temperature; open circles, speeds measured during decreasing temperature; dotted lines indicate 48-hr interval.

RESULTS

Swimming speed

Low temperature: We calculated the mean daily speed by averaging the hourly medians and plotted these values against mean daily temperature (Fig. 1-A). As temperature decreased, mean speed increased until 14.3° C. From this level to 11.9° C, swimming speed nearly doubled. At this low temperature there was also a general lightening in color around the insertion of the pelvic fins. Whether this was due simply to the change in temperature as Abbott (1969) found in *Fundulus heteroclitus*, or like the marked increase in speed was indicative of stress, was not determined. We then raised the temperature 2.3° C over a 3-day period. This rise was accompanied by a rapid decrease in speed approaching that recorded at 14.3° C. Immediately following this we lowered water temperature from 14.2° C to 11.8° C over a 5-day period. This again resulted in a rapid increase in swimming speed.

As the temperature rose smoothly toward the acclimation temperature, swimming speed was depressed below that observed during the initial drop, finally coming to approach the mean speeds recorded at the acclimation temperature. Coloration at the base of the pelvic fins returned to normal.

The coefficient of variation (c.v. = $\sigma'/\bar{x} = \tilde{R}_5/2.257\bar{x}$; Ferrell, 1958) showed
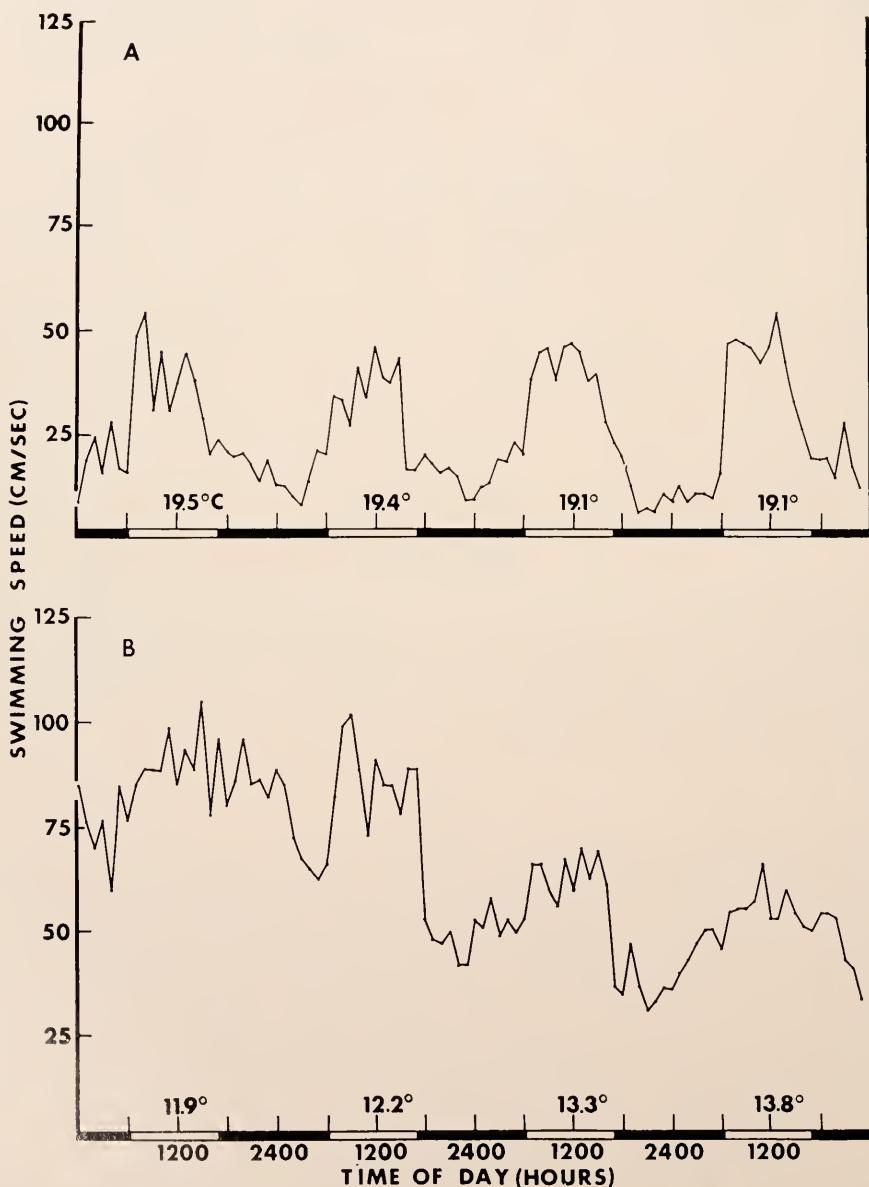

FIGURE 2. Daily swimming speed rhythm measured during low temperature experiment: (A) acclimation, (B and C) stress and gradual recovery, and (D) recovery.

FIGURE 2—Continued
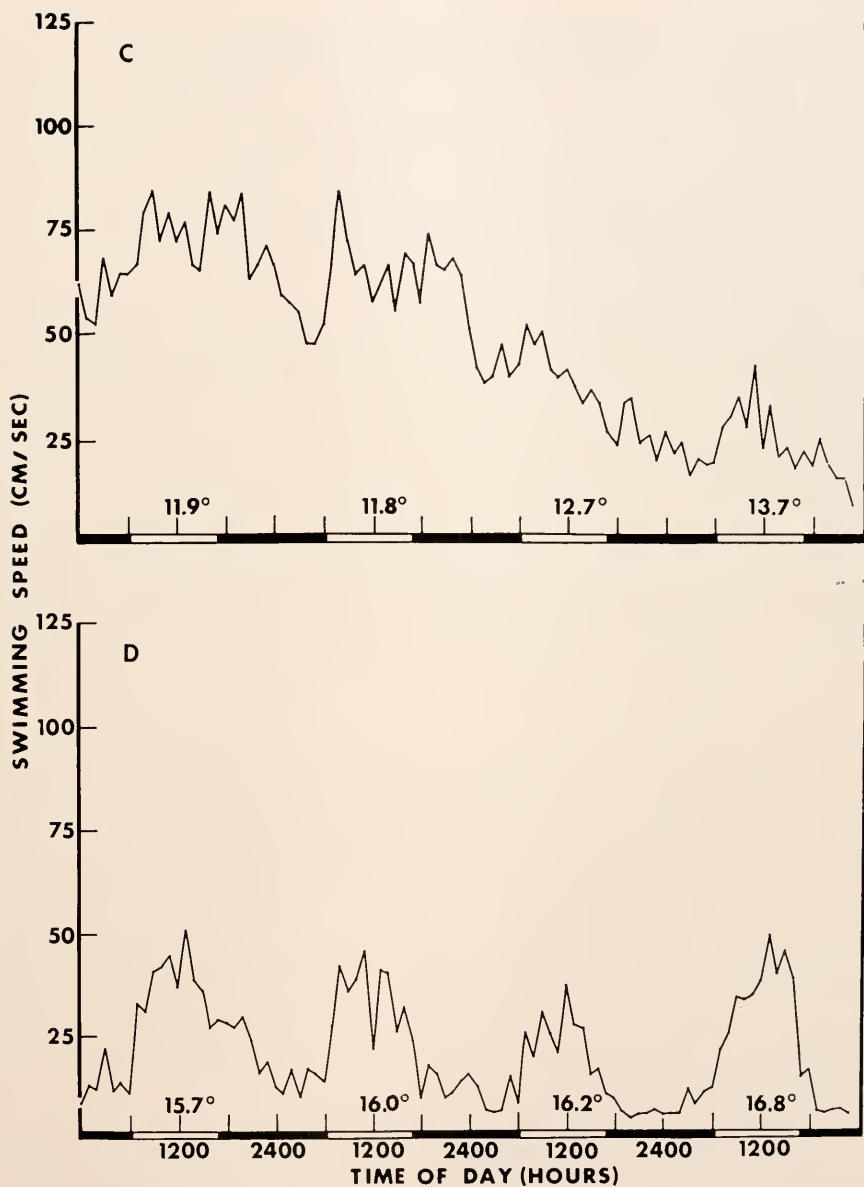
that the inherent minute-to-minute variability in swimming rate at the acclimation temperature was higher at night (c.v. = 22.0%) than during the day (c.v. = 13.6%). When the temperature reached 11.9° C, analysis showed that under stress, minute-to-minute variation decreased during both day (c.v. = 9.6%) and night (c.v. = 12.4%), the greater change occurring at night. As the temperature

rose to 12.7° C following the second stress period, variation during the day (c.v. = 11.3%) and night (c.v. = 11.2%) were essentially the same.

High temperature: As the temperature increased to 29.3° C, mean speed gradually increased (Fig. 1-B). When the temperature reached 29.8° C, swimming speed increased rapidly within a 24-hr period. Speeds remained relatively high while the temperature was held at 30.4° C. There was also a marked increase in the opening of the mouth and opercula. Similar to findings by Cocking (1957, 1959a) on roach (*Rutilus rutilus*) at stress temperatures, body color above the lateral line darkened. These changes along with the increase in speed we considered to be indicative of stress.

As temperature dropped from 30.4° C to 28.1° C, swimming speed decreased rapidly. As was true following stress at low temperatures, swimming speed was depressed below levels recorded during the period of temperature rise. Near the acclimation temperature, swimming speed approached pre-test levels. Coloration returned to normal as did the gape of the mouth.

At the acclimation temperature of 19.9° C, there was a higher degree of minute-to-minute variability in swimming speed at night (c.v. = 18.9%) than during the day (c.v. = 10.5%). When the temperature reached 29.8° C, variability in speed decreased under dark conditions (c.v. = 13.2%), and increased slightly during the day (c.v. = 14.7%); *i.e.* differences between day and night almost disappeared. In contrast with recovery from low temperature stress, variation increased markedly both day (c.v. = 17.5%) and night (c.v. = 27.8%), well above that observed at 19.9° C.

Daily rhythm of swimming speed

Low temperature: As the temperature decreased and the speed gradually increased, the daily rhythm persisted until the temperature fell below 12.0° C (Fig. 2, A–B). At this point the fish swam at significantly greater speeds at night with consequent diminution of the rhythmic pattern although there were still significant differences between day and night (P < 0.05; Tukey-Duckworth End Count Test, Tukey, 1959). As the temperature rose above 12.0° C, speeds decreased and a well-defined daily rhythm was evident. As the temperature dropped below 12.0° C for a second time (Fig. 2-C), the fish resumed swimming at high speeds both day and night and for a period of about 41 hours, there was no significant difference between day and night (P > 0.05). Unlike the previous temperature recovery period, there was still no significant separation of day and night speeds (P > 0.05) until the temperature went above 12.7° C (Fig. 2, C–D).

High temperature: As the temperature rose and the mean speed increased, the daily rhythm persisted until the temperature reached 30.4° C (Fig. 3, A–B). Then as we had observed at low temperature stress levels, there was no significant difference betwen day and night speeds for 48 hours (P > 0.05; Tukey-Duckworth End Count Test). Although the mean daily temperature remained at 30.4° C for the two following days, significant day-night differences reappeared (P < 0.01). As the temperature dropped below 30.4° C and swimming speeds dropped sharply, there was no significant day-night difference for 24 hours (P > 0.05). Then throughout the rest of the temperature recovery, *i.e.*, as the temperature dropped below 28.1° C, a daily rhythm was evident (Fig. 3-C).

TABLE I

Day-night schooling tendency as related to changing temperature

	Low temperature							High temperature					
Avg. temp. °C	Schooling index* Night	Day	Δ = D-N	III compared to I	II	IV	Avg. temp. °C	Schooling index* Night	Day	Δ = D-N	III compared to I	II	IV
19.5	2.5	4.4	+1.9	+			19.9	2.7	4.8	+2.1			
19.4	1.8	3.4	+1.6	+			20.0	1.5	5.9	+4.4	+		
19.1	1.5	4.3	+2.8	+			20.0	2.6	5.9	+3.3	+		
I 19.1	2.2	5.4	+3.2	+			19.8	2.1	5.7	+3.6	+		
18.8	3.5	5.5	+2.0	+			I 20.3	2.5	5.7	+3.2	+		
18.5	2.2	4.1	+1.9	+			20.6	2.1	5.5	+3.4	+		
17.9	2.3	5.0	+2.7	+			20.9	4.3	5.8	+1.5			
17.0	4.1	5.9	+1.8	+			21.8	2.4	5.6	+3.2	+		
							22.3	1.7	5.5	+3.8	+		
							22.7	1.7	5.6	+3.9	+		
15.7	3.9	5.4	+1.5		+								
15.4	3.4	4.4	+1.0		+								
15.3	2.7	5.9	+3.2		+		23.1	2.9	5.5	+2.6		+	
II 15.1	3.3	4.9	+1.6		+		23.6	2.2	5.8	+3.6		+	
14.9	4.3	5.5	+1.2		+		24.4	3.0	5.5	+2.5		+	
14.9	2.5	4.8	+2.3		+		24.5	3.1	5.9	+2.8		+	
14.7	3.4	5.7	+2.3		+		II 25.2	2.5	5.8	+3.3		+	
14.3	4.6	5.9	+1.3		+		25.8	2.9	5.8	+2.9		+	
							26.4	4.3	6.0	+1.7			
11.9	5.8	6.0	+0.2	−	−	−	26.6	4.0	5.9	+1.9			
12.2	6.0	5.6	−0.4	−	−	−	27.3	2.1	5.7	+3.6		+	
III 13.3	5.5	5.9	+0.4	−	−	−	27.8	2.3	5.1	+2.8		+	
13.8	5.3	5.9	+0.6	−									
11.9	5.7	5.8	+0.1	−	−	−	28.4	5.2	6.0	+0.8	−	−	
11.8	5.9	5.7	−0.2	−	−	−	28.7	5.2	5.7	+0.5	−	−	
							29.3	5.3	5.8	+0.5	−	−	
12.7	3.7	5.5	+1.8			+	III 29.8	5.7	6.0	+0.3	−	−	−
13.7	2.3	3.7	+1.4			+	30.4	3.8	6.0	+2.2			
IV 15.7	2.2	4.9	+2.7			+	30.4	5.0	5.0	0	−	−	−
16.0	2.5	5.5	+3.0			+	30.4	5.5	5.8	+0.3	−	−	
16.2	1.5	4.8	+3.3			+	30.4	5.2	6.0	+0.8	−	−	
16.8	1.5	5.5	+4.0			+							
							28.1	3.0	5.6	+2.6			+
							26.9	3.1	5.7	+2.6			+
							25.7	2.1	4.4	+2.3			+
							IV 24.9	1.9	5.4	+3.5			+
							22.5	1.4	4.5	+3.1			+
							22.0	2.5	5.0	+2.5			+
							21.9	3.1	3.9	+0.8			
							21.4	3.2	3.7	+0.5			
Sign test			26 + / 2 −							35 + / 0 −			
End Count test				8 6	8 6	6 6					8 7	8 7	6 3
P ≤			0.01	0.001	0.001	0.01				0.01	0.001	0.001	0.01

* Schooling index = $\sum$ (freq. 6 fish × 6 + freq. 5 fish × 5 . . . freq. 1 fish × 1)/100 where frequency = % of occurrence of each group size measured 5 times each hour.

Schooling

Low temperature: Similar to our findings under normal conditions (Olla and Studholme, 1972), the tendency to school throughout the experiment was significantly greater during the day than at night ($P < 0.01$; Sign Test; Table I). At
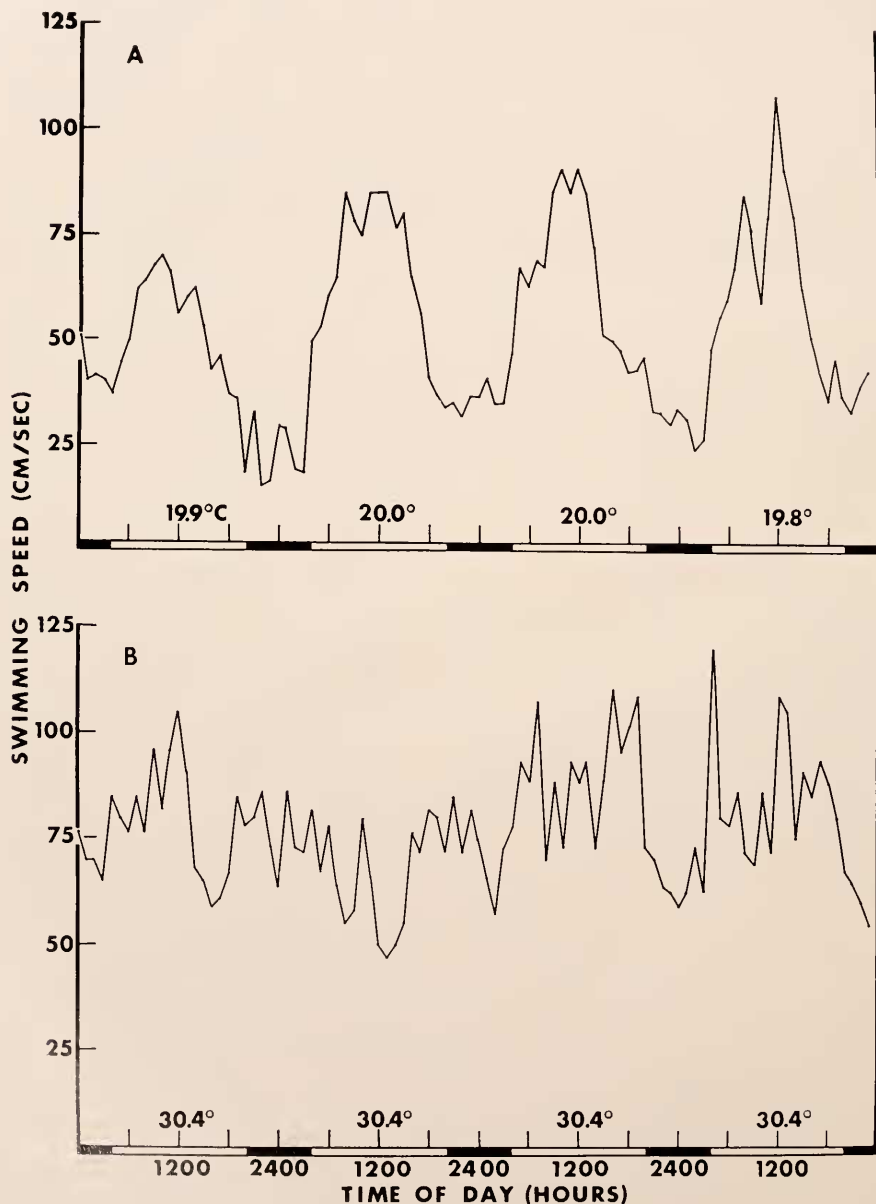

FIGURE 3. Daily swimming speed rhythm measured during high temperature experiment: (A) acclimation, (B) stress, and (C) recovery.
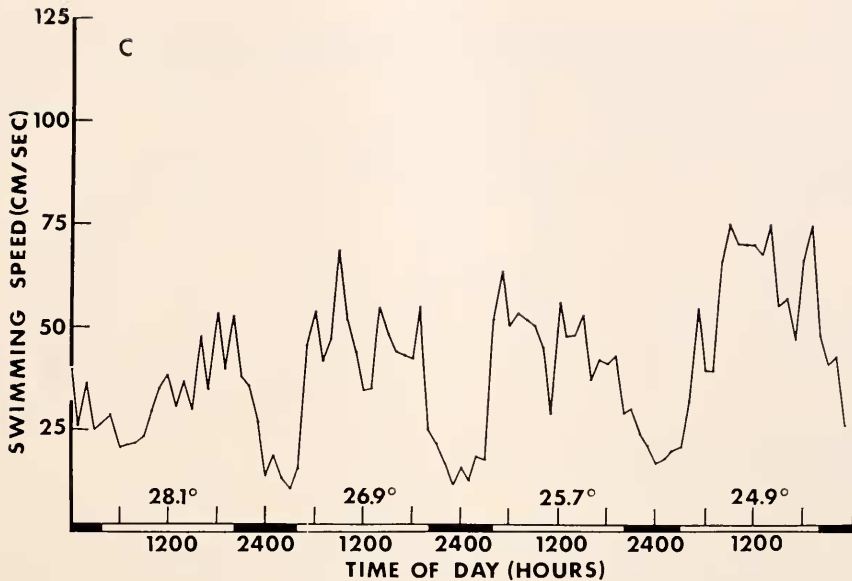
FIGURE 3—*Continued*

a temperature of 11.9° C, night schooling increased. The difference in the tendency to school between day and night was significantly reduced at low stress temperatures ($P < 0.01$; Tukey-Duckworth End Count Test).

High temperature: Throughout the experiment, schooling tendency was again significantly greater during the day than at night ($P < 0.01$; Sign Test; Table I). When the temperature reached 28.4° C, schooling tendency increased significantly at night, reducing day-night differeneces ($P < 0.01$; Tukey-Duckworth End Count Test). Towards the end of the temperature recovery, small day-night differences reappeared.

Feeding

Low temperature: Feeding, as measured by the quantity of food ingested, was relatively stable until the temperature dropped to 13.7° C at which point there was a 40% decrease compared with amounts taken during acclimation (Table II). Feeding remained low following stress temperatures and then increased slightly as the temperature rose.

High temperature: Feeding fluctuated considerably as the temperature increased to 30.2° C (Table II). Following the 6-day period of constant temperature of 30.4° C, feeding decreased and showed no appreciable increase as the temperature returned toward acclimation levels.

DISCUSSION

The most discernible response to both high and low temperature stress was the increase in swimming speed by about $3\frac{1}{2}$ times above acclimation speeds at low temperature stress and $1\frac{1}{2}$ times above acclimation speeds at high temperature

TABLE II

Weight of live prey ingested as related to temperature changes

Low Temperature*		High Temperature**	
Avg. temp. °C	Grams taken	Avg. temp. °C	Grams taken
19.0	2180	20.0	2399
16.6	2070	22.2	3136
15.0	2210	24.2	1973
13.7	1310	26.1	2586
14.1	1470	28.3	2324
15.1	1810	30.2	1963
16.9	1750	30.4	1442
		24.1	1440
		21.2	1513

* Feeding intervals 7 days.
** Feeding intervals 6 days.

stress.   The speed increase with increasing temperature probably was less than that at decreasing temperature because the initial average speed was high due to the seasonal effect of longer photoperiods (Olla and Studholme, 1972).   Since this seasonal effect would tend to complicate a comparison of the rate of change in swimming speed, it is possible that had both experiments been conducted under the same photoperiod the rate of increase might have been similar.   However, average speeds at both stress levels were of the same magnitude, *i.e.*, about 70–80 cm/sec. It is likely that the lower speeds observed at acclimation presumably are normal for bluefish at that temperature and at those photoperiods.

The decrease in well-defined patterns of rhythmicity at stress temperatures was due to a decrease in the difference between day and night speeds.   The peak-to-trough differences diminished as a result of proportionately greater increases in night speeds.   Other indications of response to stress were also clearly evident at night.   Variation in speed, usually high at night, was significantly less.   Schooling tendency, normally low, showed a significant increase, approaching daytime levels. Whether the increase in schooling tendency at night at thermal stress levels is the result of the increase in swimming speed or is due to a direct change in fish-to-fish responsiveness could not be determined.

In contrast to the similarity in the responses of the fish to both cold and hot temperature stress were several differences observed when the temperature was returning to acclimation levels.   Following low temperatures, the day-night school-ing pattern returned to normal; following high temperatures, after an initial return to normal schooling patterns for about 10 days, there was a sharp decrease in day-night differences matching those observed under stress.   Feeding gradually in-creased during temperature recovery from low stress but remained relatively low for at least two feeding sessions following high temperatures.

Depressed speeds, abnormal schooling tendency and feeding following exposure to high temperatures may indicate, that while the external source of stress has been removed, the animal has in effect not really returned to normal.   This could be

the result of a delay in acclimation related to the exposure to stress. Fish subjected to high temperatures and then returned to non-stress conditions may be more susceptible to predation (Coutant, 1970a), disease (Cairns, 1956), and less able to function as successful predators. Cairns (1956) found that though feeding in bluegill (*Lepomis macrochirus*), pinfish (*Lagodon rhomboides*) and channel catfish (*Ictalurus punctatus*) increased, the fish became emaciated following prolonged exposure to "sub-lethal" temperatures. Our results showed no consistent change in feeding during the experiment except following stress temperatures when prey capture decreased.

Peterson and Anderson (1969), in their work on Atlantic salmon (*Salmo salar*), found that regardless of the direction of temperature change, locomotor activity increased. Their experiments showed that it was the rate (from about 0.1–0.7° C/min) rather than just the amount of change which influenced the increase in activity. In our own work, the slow rate of temperature change would probably negate any strong influence of rate on change in activity. Although Cocking (1959b) states that a rate of 1/20° C/hr temperature increase was sufficient to permit continual acclimation in roach, it is our feeling that there may be a delay in the acclimation of the bluefish to both the increase and decrease in temperature. In current work on Atlantic mackerel (*Scomber scombrus*), swimming activity continued to increase for several time constants although the temperature increase (0.5° C/day) was stopped well below lethal levels. This would indicate that although the rate of increase was low, a delay existed in the acclimation of the animals (Olla, in preparation). However, in our findings on bluefish, presumably any delay is slight and constant so that the observed responses, at least at the upper levels, can be related to specific temperatures.

Thermal limits established here are only relevant to the particular size range under study. We would expect, as has been noted for other species, that differences in temperature responses would be dependent on size and age (de Sylva, 1969).

Since seasonal changes in photoperiod affect thermal lethal limits (Hoar and Robertson, 1959; Tyler, 1966; Graham, 1970), it is essential that these results be considered relative to photoperiod. Additionally, since these limits were based on the responses of slowly acclimated animals, animals subjected to rapid temperature changes in the environment, due to natural or unnatural causes, would respond at different thermal levels, dependent on the acclimation temperature and season.

There are basic differences in the responses of pelagic and benthic fishes to temperature extremes. For example, puffer (*Sphaeroides maculatus*) are highly unresponsive at night, normally lying quiescent on the bottom. Wicklund (1970) states that a massive kill of puffer which occurred during an abnormal temperature drop at night may have been due to this low level of responsiveness. In field studies on another benthic species, winter flounder (*Pseudopleuronectes americanus*), Olla, Wicklund and Wilk (1969) found that these fish, normally day-active, became inactive as the temperature rose above 22.3° C. Laboratory studies on summer flounder (*Paralichthys dentatus*) showed that when subjected to temperature drops averaging 3° C/hr, this semi-benthic fish became quiescent with a drop in the cardiorespiratory rate of more than 50% (Olla and Wicklund, unpublished). In contrast, some pelagic species such as the bluefish and many of the scombrids,

must swim continually to (1) maintain hydrostatic equilibrium due to an insufficient or absent swim bladder (Magnuson, 1970); (2) ventilate the gills (Hall, 1930; Magnuson, 1963); or (3) aid in venous circulation through continued contraction of skeletal musculature. These fish react to stress temperatures with increased responsiveness. The nature of the response to both low and high temperature extremes may serve to move the animals out of areas of adverse temperature. Lund and Maltezos (1970) state that when the water temperature falls below 15° C, adult bluefish begin their fall migration. This relates to our findings of generally high speeds at temperatures below 15° C.

We wish to express our grateful appreciation to Enoch B. Ferrell for his advice on the statistical treatment of the data.

SUMMARY

1. The swimming speed of the bluefish increased as temperature increased or decreased from acclimation levels of 19–20° C.
2. As the temperature approached 11.9° C and 29.8° C, there were significant changes in average swimming speed and schooling which were considered to be indicative of stress.
3. The daily rhythmic activity was not well-defined at stress temperatures.
4. As the temperature departed from stress levels toward acclimation, swimming speed dropped significantly and the daily rhythm of activity returned.

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